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DELIMITATION AND SUBDIVISION OF THE ACANTHACEAE

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THE DELIMITATION OF THE FAMILY

In the paper of 1942 in which I discussed the position of the genus *Thomandersia* Baill. (Rec. d. trav. bot. Neerl. 39 : 166-175, 1942) I still accepted in conformity with Bentham in Bentham and Hooker, Genera Plantarum, and with Lindau in Engler and Prantl, Naturliche Pflanzenfamilien IV, 3 b, the *Acanthaceae* in the delimitation which had been given to them by C. G. Nees von Esenbeck in De Candolle, Prodromus 11, 1847. These authors were all fully convinced that the *Acanthaceae* formed in that delimitation a natural unit, which means that the groups of genera which were included by them in this family were, in their opinion, more closely related with each other than with any group of genera which had been included in another family. This idea was subsequently abandoned by me (the Delimitation of the *Acanthaceae*, Proc. Kon. Ned. Akad. v. Wetensch. Ser. C, 56 : 533-546, 1953), as a more detailed study of the various groups of genera had convinced me that Lindau's *Thunbergioideae* and *Mendoncioideae* show a greater affinity with the *Bignoniaceae* and *Pedaliaceae* than with his *Acanthoideae*, and that his *Nelsonioideae* are nearly related to the *Rhinantheae*, and are therefore to be transferred to the *Scrophulariaceae*, at least if the *Rhinantheae* are regarded as belonging to that family. However, if the *Rhinantheae* are accepted as a distinct family (*Rhinanthaceae*), the *Nelsonioideae* will have to be included in the latter. For our present purpose this is a point of minor importance, as this family at any rate would have to be regarded as more nearly related with the *Scrophulariaceae* than with the *Thunbergiaceae, Mendonciaceae, Acanthaceae, Bignoniaceae* and *Pedaliaceae.*

The exclusion of Lindau's *Nelsonioideae, Thunbergioideae* and *Mendoncioideae* enables us, as had been recognized already by van Tieghem (Annales des Sciences, Botanique Ser. 9, 7, 1908), to give a satisfactory definition of the *Acanthaceae,* and this is something in which the earlier authors did not succeed. In the new delimitation the *Acanthaceae* are a family of the *Tubiflorae* which on account of the zygomorphic androecium and the exalbuminous seeds is to be regarded as nearly related to the *Thunbergiaceae, Mendonciaceae, Bignoniaceae* and *Pedaliaceae,* and I may add here to the *Martyniaceae* and *Henriqueziaceae* (cf. Bremekamp, Acta Bot. Neerl. 6 : 351-377, 1957), but differing from them by the presence in the ovary cells of two or more ovules, which in the latter case are arranged in two or, very rarely, four longitudinal rows inserted near the middle of the dissepiment, by the loculicidal capsule which dehisces elastically, the dissepiment being split at the same time in two parts which remain, partly or entirely, attached to the valves, and by the more or less distinctly flattened seeds subtended by usually well-developed retinacula.

B. M. Johri and Hardev Singh (Botaniska Notiser 112 : 248, 1959) object to this definition, observing that "The seeds are said to be flat, but in *Andrographis* (Acanthaceae) they are round (Mauritzon, 1934)". Mauritzon, however, was mistaken ; the seeds of *Andrographis,* although not very thin, are distinctly flattened. It is perhaps worthwhile to point out that the observations made by Mauritzon (Die Endosperm- und Embryoentwicklung einiger Acanthaceen, Lunds Universitets Aorsskrift 30, no. 5, 1934) on the seed structure of this genus are, owing to the fact that no young seeds were available to him, very incomplete, and that the conclusions which he drew from them, are entirely unacceptable. He says (p. 34) "Wuerde sich meine Annahme einer aehnlichen Entwicklung wie bei *Thunbergia* als richtig herausstellen—was sehr wahrscheinlich ist—so deutet dies auf eine isolierte Stellung fuer *Andrographis* in die Unterfamilie *Acanthoideae* und es waere eine Ueberfuehrung in die Unterfamilie *Thunbergioideae* zu erwaegen, insoferri nicht andere wichtige systematische Charaktere dagegen sprechen." However, for the assumption that the development of the endosperm of *Andrographis* would be similar to that of the endosperm of *Thunbergia* no arguments are adduced, and his remark that his assumption will probably be right, is therefore of no value whatsoever. For a transfer of *Andrographis* to the *"Thunbergioideae"* there is no ground at all, for all the above mentioned characters of the *Acanthaceae* s.s. and not one of those of the *Thunbergiaceae* are found in this genus.

The *Thunbergiaceae* sensu meo (l.c. p. 540) are recognizable by the rostrate capsule provided with one or two seeds in each of the two cells and by the shape of the seeds, which are semiglobose and at the ventral side provided with a large excavation. In the presence of an epicalyx formed by the two very large bracteoles and in the truncate, dentate or shortly lobed calyx this family resembles the *Mendonciaceae.* Another point of resemblance is the presence of a curious kind of bristles at the base of the anthers. In the *Mendonciaceae* these bristles are apparently a general feature, but in the *Thunbergiaceae* they are found only in the subgenus *Coniostephanus* of *Thunbergia* (cf. Bremekamp, The Thunbergia Species of the Malesian Area, Verh. Kon. Ned. Akad. v. Wetensch., afd. Natuurk. 2nd Ser. 50, no. 4, 1955, p. 13).

The *Thunbergiaceae* are confined to the Old World, where they are represented by three genera, viz. *Thunbergia, Pseudocalyx* and *Meyenia.* The inclusion of the African genus *Pounguia* does not seem to be justified, but the exact position of this genus is still unknown.

The *Mendonciaceae* (l.c. p. 540) are recognizable by their drupaceous fruits, which usually are unilocular and provided either with one or with two seeds, and by the pollen grains with their very short colpi and their very thick nexine ; such pollen is, as far as I know, confined to this family.

The *Mendonciaceae* are best represented in tropical America, but they are found also in Tropical West Africa and in Madagascar.

In my paper of 1953 I drew the attention to a little known character which the *Acanthaceae* s.s. have in common with the *Thunbergiaceae* and the *Mendonciaceae,* viz. the presence of "raphidines" (l.c. p. 537), a peculiar kind of fibres that are formed inside certain cells of the phloem. Their occurrence is, as I pointed out, rather erratic, "for in some genera and species they are found in large numbers, whereas in others they are fairly rare or confined to special parts like the petiole or the root." These elements have not been found in the *Nelsonieae* (l.c. p. 538). However as they are rather rare in some of the genera belonging to the three families mentioned above, there is a slight possibility that they have been overlooked in the *Nelsonieae,* of which but a few species were investigated, as well as in the related families (*Bignoniaceae, Henriqueziaceae, Martyniaceae, Pedaliaceae*).

The three families *Acanthaceae, Thunbergiaceae* and *Mendonciaceae* are now well-defined, and this can also be said of the *Henriqueziaceae* and *Martyniaceae,* but not of the *Bignoniaceae* and the *Pedaliaceae.* In discussing the position of the genus *Thomandersia* (see the paper quoted above, p. 171) I said of the *Bignoniaceae* that they are a rather vaguely circumscribed family, but that some of the tribes are much better defined. This means apparently that its naturalness is rather doubtful. A tribe like that of the *Crescentieae* shows so little resemblance with the other ones that its inclusion seems hardly justified, and between the remaining tribes too the differences are by no means negligible. This applies also to the *Pedaliaceae* of which I remarked (l.c. p. 172) "The general characters of the *Pedaliaceae* too are vague, and even after the exclusion of the aberrant genus *Trapella* Oliv. they remain difficult to grasp", and I added that in surveying the diagnosis of the family given by Stapf (in Engler and Prantl, Naturl. Pflanzenfam. IV. 3 b) we find hardly any difference with that of the *Acanthaceae* given by Lindau in the same volume of Engler and Prantl. However, this is no longer so if the *Acanthaceae* are accepted in the delimitation proposed by me, for all the more important points of resemblance between the *Pedaliaceae* and the *Acanthaceae* in their original delimitation prove to be confined to part of the latter, viz. to the two subfamilies which have been raised by me to family rank, the *Thunbergiaceae* and the *Mendonciaceae.*

My view that Lindau's *Thunbergioideae* and *Mendoncioideae* are to be raised to family rank, has raised no protest so far, but my opinion with regard to the position that is to be assigned to his *Nelsonioideae,* has been challenged by B. M. Johri and Hardev Singh in their paper on "The morphology, embryology and systematic position of *Elytraria acaulis* (Linn. f.) Lindau", to which reference has already been made. On p. 235 they state "Bremekamp's (1953, 1955) report of the absence of a jaculator in *Elytraria* is incorrect." They base this rejection of my statement apparently on what they have seen in the sagittal sections shown in their figures 47-50, where on the micropylar side of the funicle as well as on the opposite side a swelling is seen ; the first they call an obturator, the second a jaculator, i.e. a retinaculum. However, if they had made longitudinal sections perpendicular to the sagittal plane, they would have seen similar swellings, one at the left and one at the right side of the funicle ; and if they had looked at the funicle of an intact ovule, they would have seen what these "swellings" really are. In that case it would have been clear to them that there is in *Elytraria* neither a retinaculum nor an obturator, but that the funicle is in its upper part equally dilated in all directions. In fact, there is in *Elytraria* nothing which could be compared with the hooklike excrescence of the funicle which is found in the true *Acanthaceae,* and which is known as the retinaculum.

On p. 247 they compare the characters of *Elytraria,* which is assumed to represent the *Nelsonieae,* with those of the *Acanthaceae,* which are apparently taken in the delimitation proposed by me, for they are said to be erect herbs or shrubs provided with thick-walled loculicidal capsules with explosive dehiscence, a definition which excludes the *Thunbergiaceae* and the *Mendonciaceae,* and with those of the *Rhinantheae.* The characters have, unfortunately, been taken for a considerable part from the older literature, which is by no means always trustworthy. For this reason I will subject their table to a detailed criticism. For the sake of brevity the *Nelsonieae* will be indicated in the following exposition by the figure 1, the *Acanthaceae* by 2, and the *Rhinantheae* by 3.

Habit : 1. Rosette herbs with alternate leaves ; 2. erect herbs or shrubs with opposite leaves ; 3. semi-parasites with alternate or opposite leaves. Here it may be objected that the *Nelsonieae* are by no means all rosette herbs with alternate leaves ; in fact, this description applies to the genus *Elytraria* only ; in the other genera we find a leafy stem with opposite or towards the top alternate leaves, but the bracts are indeed always alternate, and this is a rather important point, as the bracts of the *Acanthaceae* are always, just as their leaves, opposite. That the *Rhinantheae* are hemi-parasites does not mean very much, as in some other tribes of the *Scrophulariaceae* hemi-parasites and entirely autotrophic plants occur side by side ; moreover, only of the more common genera of the *Rhinantheae* we know with certainty that they live as hemiparasites.

Inflorescence : 1. Scapigerous, racemose ; 2. cymose ; 3. cymose. A scapigerous inflorescence is in the *Nelsonieae* found only in *Elytraria,* and this character is therefore in this connection of no importance. In the majority of the *Acanthaceae* the inflorescence is not cymose but racemose, and in the *Rhinantheae* the flowers are either axillary or racemosely arranged ; cymose inflorescences are not known to me in this tribe.

Placentation : 1. Parietal ; 2. axile ; 3. axile. I see no difference in the way in which the ovules in these three groups are inserted, nor can I find any indication of a parietal placentation in the figures given by the authors.

Pollen grains : 1. 3-colporate (syncolpate), shed at the 2-celled stage ; 2. 2- to 6-colpate, shed at the 2- to 3-celled stage ; 3. 2- to 7-colpate (syncolpate), shed at the 2-celled stage. The description of the pollen grains of the *Nelsonieae* as syncolpate is correct, that they are 3-colporate is a mistake ; they are always 3-colpate (see Bhoj Raj, Grana Palynologica 3 : 23, 1961) ; the pollen grains of the *Acanthaceae* are sometimes colpate and sometimes colporate or porate. In the structure of the pollen grains there is no definite indication either for an affinity with the *Acanthaceae* or for an affinity with the *Rhinantheae.*

Ovule : 1. Unitegmic, tenuinucellate, amphitropous with a funicular obturator and a jaculator ; integumentary tapetum present ; 2. unitegmic tenuinucellate, anatropous with a jaculator ; funicular obturator and integumentary tapetum absent ; 3. unitegmic, tenuinucellate, amphitropous ; integumentary tapetum present. That a funicular obturator and a jaculator would be present in the *Nelsonieae,* is, as I have pointed out already, a mistake ; there is merely an apical swelling of the funicle ; that the ovule is amphitropous and that an integumentary tapetum is present point to an affinity with the *Rhinantheae.*

Embryo sac : 1. Polygonum type ; antipodal cells persistent, often becoming binucleate ; 2. Polygonum type ; antipodal cells usually ephemeral ; 3. Polygonum type ; antipodal cells ephemeral. I see here no distinct indication either for a closer affinity with the *Acanthaceae* or with the *Rhinantheae.*

Endosperm : 1. Cellular, conforms to the Pedicularis type of Crete (1951) ; micropylar haustorium well developed ; central chamber grows asymmetrically and lacks the free nuclear phase ; 2. cellular ; micropylar and chalazal haustoria present ; central chamber grows asymmetrically and has a free nuclear phase ; 3. cellular, conforms to the Pedicularis type ; micropylar and chalazal haustoria well developed ; central chamber grows symmetrically and lacks the free nuclear phase. In the early segmentation of the endosperm (Pedicularis type) and in the absence of the free nuclear phase there is agreement with the *Rhinantheae* and disagreement with part of the *Acanthaceae* (in the *Acanthoideae* s.m. a free nuclear phase may be present), in the asymmetrical development of the central chamber there is, on the contrary, agreement with the *Acanthaceae,* but whether this asymmetrical development is a general feature of the *Acanthaceae* remains to be seen : the number of genera that so far have been investigated, is far too small, and that it does not occur at all in other families, rests, as far as I can see, only on a communication by Mauritzon dating from 1934.

Embryo : 1. Conforms to Lythrum-variation of Onagrad type ; 2. conforms to Lythrum-variation of Onagrad type ; 3. conforms to Pedicularis-variation of Onagrad type. One of the terms by means of which the different embryo types are indicated, viz. the Pedicularis-variation of the Onagrad type, proves already that similar embryo types occur in taxonomically entirely unrelated groups. The taxonomic value of such similarities is therefore negligible.

Seed : 1. Albuminous, endosperm ruminate ; testa absent ; 2. exalbuminous ; testa well developed ; 3. albuminous ; testa well developed. The presence of a persistent endosperm indicates doubtless a much closer affinity with the *Rhinantheae* than with the *Acanthaceae*. Whether the testa is entirely absent in *Elytraria* is difficult to say, but in the other genera of the *Nelsonieae* it is certainly not absent ; in *Nelsonia* it bears the curious "hammer-headed hairs", which as I have shown elsewhere (Reinwardtia 3 : 246, 1955), are no hairs at all, but bars that are set free when the outer wall of the testa cells is torn asunder. The form of the seed is not mentioned by the authors, but here we find complete agreement with the *Rhinantheae,* and disagreement with the *Acanthaceae,* where the seeds are always flattened.

Fruit : 1. Thick-walled, capsule with explosive dehiscence ; 2. thick-walled, loculicidal capsule ; explosive dehiscence ; 3. thick-walled, loculicidal capsule. Apart from the presence of retinacula in the capsule of the *Acanthaceae,* there is also the curious structure of the solid tip, of which the cells in the usually hygrochastic fruits are severed from each other when the desiccated capsule is moistened. A solid tip of this kind is met with neither in the *Nelsonieae* nor in the *Rhinantheae.*

From the remarks which I have made above, it will be clear that the comparative table compiled by Johri and Singh contains too many inaccuracies to be of decisive value in the question of the position which is to be given to the *Nelsonieae,* and that it certainly does not justify their conclusion that my transfer of this tribe from the *Acanthaceae* to a position in the vicinity of the *Rhinantheae* is to be rejected. Their remark that I have transferred the *Nelsonieae* "to the subfamily Rhinanthoideae, tribe Rhinantheae of the Scrophulariaceae", moreover, is incorrect. In reality I rejected the present subfamily *Rhinanthoideae* as unnatural, and proposed a new subfamily of this name with two tribes only, the *Rhinantheae* and the *Nelsonieae.* That the latter cannot be included in the *Rhinantheae* was perfectly clear to me, as is proved by the following quotation from my paper of 1953 (p. 545). "At the moment the best solution seems to be to give the *Nelsonioideae* a place in the vicinity of the *Rhinantheae* as a tribe *Nelsonieae,* but then the subdivision of the family on account of the aestivation of the corolla lobes will have to be dropped, for in the present subfamily *Rhinanthoideae* there is certainly no place for them." In the diagnosis of the tribe *Nelsonieae* given on the same page I stated moreover that this tribe differs from the *Rhinantheae* in the descending aestivation of the corolla lobes, in the fact that the upper lip is never galeate, and in the firmer structure of the capsule wall. Elsewhere on the same page I mentioned moreover the shortness of the funicle and the mode of life, the hemiparasitism of the *Rhinantheae* being unknown in the *Nelsonieae.* This point has been discussed already.

However, at this juncture the resemblance between the *Nelsonieae* and the *Rhinantheae* is of more importance than their points of difference. I mentioned l.c. the presence of a well-developed endosperm, a character of great taxonomic importance in which they differ not only from the *Acanthaceae* s.s. but also from the nearest allies of the latter, the *Thunbergiaceae, Mendonciaceae, Bignoniaceae, Henriqueziaceae, Pedaliaceae* and *Martyniaceae,* the type of placentation, in which these two tribes differ from the other *Scrophulariaceae,* and the loculicidal capsule, two points in which they resemble the *Acanthaceae* s.s., and in the globose seeds, in which they differ very conspicuously from the *Acanthaceae* s.s., where the seeds always are more or less distinctly flattened. In the structure of the capsule the resemblance with the *Acanthaceae* s.s. is nevertheless not so complete as the above statement suggests, for the capsule of the *Nelsonieae* and the *Rhinantheae* differs from that of the latter in the absence of the curiously structured tip of which I have spoken above. The table of Johri and Singh shows moreover that the two tribes resemble each other also in the amphitropous ovule, another point in which they differ from the *Acanthaceae* s.s.

I believe that I may summarize the exposition given above by concluding that Johri and Singh did not advance valuable arguments for returning the *Nelsonieae* to the *Acanthaceae,* and that their own findings on the contrary support my view that they are nearly related to the *Rhinantheae,* and have therefore to be included in the *Scrophulariaceae,* at least so long as the *Rhinantheae* are left in that family.

After the exclusion of Lindau's *Thunbergioideae, Mendoncioideae* and *Nelsonioideae,* the remaining genera (Lindau's *Acanthoideae*) form an easily definable group, the *Acanthaceae* sensu meo. They possess a bilocular ovary, within each locule either two superposed ovules or two, exceptionally four, longitudinal rows of ovules, a loculicidal capsule which dehisces elastically, the dissepiment being split in two halves, and flattened exalbuminous seeds supported by retinacula.

THE SUBDIVISION OF THE FAMILY

The *Acanthaceae* sensu meo comprise two subfamilies, the *Acanthoideae* sensu meo, which is a much smaller group than that of Lindau, and the *Ruellioideae* (cf. Bremekamp in Proc. Kon. Ned. Akad. v. Wetensch., ser. C. 58, 163, 1955). In the *Acanthoideae* the shoots are never articulated, cystoliths are always absent, the number of stamens is always 4, the anthers are always monothecous, and the pollen grains are usually colpate, the only exception being found in the subgenus *Sphaerostenandrium* Lindau of *Stenandrium* Nees, where they are spheroidal with indistinct apertures, which are perhaps better described as "leptomata". In the *Ruellioideae*, on the other hand, the shoots are always articulated, cystoliths are always present, the number of stamens is either 4 or 2, but if there are 4 stamens at least 2 of them are provided with bithecous anthers, and the pollen grains are always provided with distinct pores, i.e. they are either colporate or porate.

The difference in the structure of the anthers is even more pronounced than the diagnoses given above suggest. This is shown in fig. 1 of the paper quoted above ; this figure shows that the two locules of the theca are in the *Acanthoideae* comparatively small and in transverse section but slightly curved, whereas the locules of the thecae of the *Ruellioideae* are much larger and in transverse section distinctly curved.

According to Mauritzon (l.c. p. 34) the endosperm of *Acanthus* and of *Crossandra,* two genera belonging to the *Acantheae,* one of the tribes of the *Acanthoideae,* and the only representatives of this subfamily that were studied by him, is from the beginning cellular, whereas the endosperm of all *Ruellioideae* investigated by him, is at first acellular. If the endosperm in the other tribes of the *Acanthoideae* would prove to be of the same type as that of *Acanthus* and *Crossandra,* this might be another difference between the two subfamilies.

In the *Acanthoideae* we may distinguish five tribes, viz. the *Haselhoffieae, Rhombochlamydeae, Stenandriopsideae, Aphelandreae* and *Acantheae.*

The *Haselhoffieae* contain but a single genus, viz. *Haselhoffia* Lindau, syn. *Physacanthus* Benth. ex C. B. Clarke[1], which is confined to Tropical Africa. This tribe differs from the other ones by the actinomorphous corolla limb with its in the bud contorted lobes. In the presence of four ovules in each of the ovary cells it agrees with the *Rhombochlamydeae.*

The *Rhombochlamydeae* (cf. Bremekamp, Acta Bot. Neerl. 4 : 645, 1955) agree with the *Haselhoffieae* in the presence of four ovules in each of the ovary cells, but show in their other characters a striking resemblance with the *Aphelandreae,* e.g. in the bilabiate corolla, and like the latter they are confined to Tropical America. The only genus, *Rhombochlamys* Lindau, is known only from Columbia. The pollen grains are prolate and 3-colpate (Bhoj Raj, Grana Palynologica 3 : 44, 1961).

The *Stenandriopsideae* (Bremekamp, Acta Bot. Neerl. 4 : 644, 1955), too, contain but a single genus which is confined to Madagascar. They resemble the *Aphelandreae* and the *Acantheae* in the presence of two ovules in each of the ovary cells, but differ from the *Aphelandreae* in the subactinomorphous corolla limb, and from the *Acantheae* in the absence of the incision at the adaxial side of the corolla throat ; in the shape of the corolla they show a rather striking resemblance to the *Haselhoffieae.* The pollen grains are globose and 3-colpate.

The *Aphelandreae* agree with the *Stenandriopsideae* and the *Acantheae* in the presence of two ovules in each of the ovary cells, of which the lower one occasionally remains rudimentary and may even be completely suppressed. They differ from these two tribes by the distinctly bilabiate corolla. The pollen grains are, as a rule, prolate and 3-colpate, but in *Stenandrium* subg. *Sphaerostenandrium* they are, as stated above, globose and provided with indistinct apertures of irregular outline. This tribe is confined to Tropical America, where it is represented by several genera.

The *Acantheae* agree with the two preceding types in the presence of two ovules in each of the ovary cells, of which the lower one may be imperfectly developed or even entirely suppressed, and differ from them in the structure of the corolla, which is zygomorphic or pseudoactinomorphic, with the two posticous lobes entirely suppressed and with a more or less deep incision at the posticous side, and in the structure of the anthers which are fringed with long hairs along the fissures. They occur in Africa, Southern Europe and throughout Tropical Asia to Polynesia, and comprise several genera.

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[1] The question whether this genus is to be called *Haselhoffia* Lindau or *Physacanthus* Benth., is difficult to decide. As Bentham did not indicate a type species, and as he did not mention that the anthers contain but a single theca and his description therefore suggests the presence of anthers of the ordinary bithecous kind, it was for a long time impossible to recognize this genus. If the unnamed species which were included by him in this genus, had not been found, it would for ever have remained a "genus incertae sedis". It became recognizable only when Clarke found Bentham's specimens in the Kew herbarium. This means that the genus became recognizable only in 1900, the year in which Clarke published his results (in the Flora of Tropical Africa), and, as Lindau had published his description of *Haselhoffia* in 1897, I am of the opinion that for this genus the name *Haselhoffia* should be accepted.

The subfamily *Ruellioideae* shows a much greater diversity than the subfamily *Acanthoideae,* and comprises a much larger number of genera and species. Provisionally I accept here the following tribes : *Trichanthereae, Whitfieldieae, Louteridieae, Ruellieae, Lepidagathideae, Andrographideae* and *Justicieae.* Three of these tribes, viz. the *Ruellieae, Lepidagathideae* and *Justicieae,* comprise several subtribes.

For the distinction of these tribes and subtribes the pollen characters are often, as was recognized already in 1883 by Radlkofer, of great importance, but they should be used with due caution, and a classification which, like that of Lindau, is based exclusively or almost exclusively on these characters is doubtless to be rejected as an artificial one. We should bear in mind that the pollen characters are not necessarily all of the same value, and that in order to determine their value the naturalness of the groups in which they occur has to be tested and their rank to be determined, and this can only be done by considering the other characters of these groups. The colpate type of pollen is doubtless in this family of great taxonomic importance, as colpate pollen is found in all *Acanthoideae* with the sole exception of *Stenandrium* subg. *Sphaerostenandrium,* and is never met with in the *Ruellioideae.* As the type of pollen which is met with in *Stenandrium* subg. *Sphaerostenandrium* is met nowhere else in this family, it is apparently to be regarded as derived from the colpate type, though the way in which it may have developed out of the latter, is as yet obscure.

In the *Ruellioideae* we find a much wider range of pollen types than in the *Acanthoideae,* and some of these types are doubtless to be regarded as fully reliable characters for the identification of some of the tribes and subtribes. This applies e.g. to those found in the *Trichanthereae, Andrographideae, Petalidiinae, Hygrophilinae, Asystasiinae, Rhytiglossinae* and *Justiciinae* ; descriptions of these pollen types will be included in the diagnoses of the various tribes and subtribes. However, not all pollen types have the same morphological value. In the *Ruelliinae* sparsiporous pollen grains and pollen grains with the pores confined to the equatorial plane occur in nearly related genera, and sometimes even in the same genus (*Dipteracanthus*), though in the latter case it is doubtful whether the delimitation of this genus has not been taken too wide. In the *Justicieae* similar observations have been made by Hallier (Ann. Jard. Bot. Buitenz. 15 : 26, 1898), who found in *Pseuderanthemum* besides species with the ordinary 3-porous pollen grains also some species with sparsiporous grains. The taxonomic value of this difference in pollen structure is therefore but slight. The same applies to the taxonomic value of an echinulate surface of the pollen grains. In the doubtless natural section of *Dipteracanthus* to which the species of the Malesian area belong, some species (e.g. *D. prostratus* and *D. repens*) have alveolate pollen, whereas some nearly related ones (*D. lanceolatus* and *D. ventricosus*) have echinulate pollen (cf. Bremekamp and Nannenga—Bremekamp, Verh. Kon. Ned. Akad. v. Wetensch., Afd. Natuurk. 2nd Sect. 44 No. 1, 1948, p. 6 and p. 15). In the *Justicieae* we find similar differences. The type species of *Asystasiella* Lindau has echinulate pollen grains, whereas those of the only other species are of the kind found in the majority of the *Pseuderanthemum* species, and in the genus *Rhacodiscus* Lindau, which by its author was referred to a subtribe *Porphyrocominae* of his *Isoglosseae,* the pollen grains of the type species as well as those of some other ones are echinulate and radially symmetric, whereas those of *Rh. secundus* (Vahl) Brem. are of the type found in *Beloperone,* i.e. distinctly flattened with a trema area studded with circular insulae (cf. Bremekamp in Bull. Torrey Bot. Club 75 : 669-670, 1948). The genus *Rhacodiscus* is apparently nearly related to *Beloperone,* and is therefore to be included in the *Justiciinae* (v. infra). The *Porphyrocominae* are a quite unnatural collection of genera which do not seem to have a single character of any importance in common. The pollen grains found in the type species of *Rhacodiscus* may perhaps be seen as a further development of the type found in *Beloperone* ; the trema area extends in them over the whole surface, and the insulae have developed into spinules.

After these preliminary remarks on the taxonomic value of the pollen characters, we will now consider the tribes and subtribes of the *Ruellioideae* separately.

The *Trichanthereae* differ from the other *Acanthaceae* by their large size and by their pollen grains. The latter are bilateral, and the two sides are ornamented with bands and provided in the middle with a pore surrounded by two thickened lips ; another peculiarity is that the bands and the lips on the two sides are oriented perpendicular to each other. The only genus mentioned by Lindau in which another pollen type was found, viz. *Macrostegia* Nees, was shown by Macbride (Candollea 5 : 402, 1934) to be identical with *Vitex,* which means that it belongs to the *Verbenaceae.* Other important characters of the *Trichanthereae* are the terminal paniculiform or racemiform inflorescence, the obtuse calyx lobes, the fleshy, actinomorphous corolla with its in the bud contorted lobes, and the glabrous seeds. They are confined to Tropical America.

The *Whitfieldieae* are provisionally retained as a distinct tribe because they do not fit at all in the group in which they were included by Lindau, viz. his *Ruellieae* (= my *Ruelliinae*). The genera belonging to the latter possess an actinomorphic or subactinomorphic corolla, whereas the *Whitfieldieae* have a strongly zygomorphic one. With regard to the structure of the pollen grains there is unfortunately no uniformity of opinion, the descriptions given by Lindau and by myself, who found but two pores, differing conspicuously from that given by Bhoj Raj (Grana Palynologica 3 : 35 and Pl. 30, figs. 11-13) in which the presence of 5 or more pores is registered. The discrepancy may perhaps be due to a misidentification of the material studied by the latter, but this is a point which cannot be settled before the material has been reinvestigated. Apart from the genera *Whitfieldia* and *Stylarthropus,* which are nearly related and have sometimes been united, the genus *Chlamydacanthus* Lindau, which by its author was included in the *Isoglossinae* (= my *Rhytiglossinae*), might belong here ; from the typical representatives of the *Rhytiglossinae* it differs rather conspicuously by the presence of four stamens and by the structure of the anthers with the thecae inserted at the same height. *Whitfieldia* and *Stylarthropus* grow on the African continent, whereas *Chlamydacanthus* has been found in Madagascar.

The *Louteridieae* were included by me in Verh. Kon. Ned. Akad. v. Wetensch 2nd Sect. 41, no. 1 : 12, 1944 in the *Ruellieae,* but on account of the rather aberrant structure of the pollen grains which was recently studied in detail by Bhoj Raj (l.c. 28, Pl. 19, figs. 1-3), it seems better to restore it to the position which it had received from Lindau. Other important characters are the fruticose habit, the paniculiform inflorescence, the fusion of the three anticous calyx lobes, the strongly zygomorphic corolla with its bulging throat and short lobes, and the two equal stigma lobes. The only known genus is endemic in Central America.

The *Ruellieae* (cf. Bremekamp, Verh. Kon. Ned. Akad. v. Wetensch., Afd. Natuurk., 2nd Sect. 41 ; no 1 : 12-16 and 30, 1944 ; Bremekamp and Nannenga —Bremekamp, op. cit. 44 no. 1 : 1-7, 1948) are a very large tribe comprising several subtribes which, however, are not yet all of them very precisely delimitated ; they are characterized by a contorted or at least not ascending aestivation of the corolla lobes and by pollen grains which are either perfectly spheroidal or ellipsoidal, and never bilateral and flattened at the poles like those of many *Justicieae* and never trigonous like those of some other representatives of that tribe, almost always provided with more than two pores, and either reticulate, spinulose or ornamented with equal and equidistant bands, very rarely (*Blechinae*) 3-colporate with the colpi united at the poles. Other noteworthy features are the decurrent outer stamens, the coalescence between the outer and the inner stamens, which is lacking only in the *Barleriinae,* the presence of dithecous anthers at least in the outer stamens, and the reduction or almost complete suppression of the posticous stigma lobe.

The *Blechinae* possess globose, 3-colporate, syncolpate pollen grains with a minutely reticulate surface, a type of pollen therefore which in the *Acanthaceae* is found in no other genus. Other important characters are the spiciform inflorescence with its large bracts, the rather small size of the flowers which do not project beyond the bracts, the actinomorphic corolla, the presence of 3-8 ovules in each of the ovary cells, and the seeds which towards the margin are densely covered with mucous hairs. *Blechum* Juss., the only genus of this tribe is confined to Tropical America, though one of its species occurs in some other tropical countries as an introduced weed.

Lindau put the genus *Blechum* in his *Petalidieae* (my *Petalidiinae*), but why he did this, is not clear. Apart from the pollen structure it differs from all the genera included in that group by its spiciform inflorescence. There is doubtless a closer resemblance to some of the genera included in the *Ruelliinae.*

The *Ruelliinae* have globose, reticulate or, more rarely, spinulose pollen grains which are usually provided with 3 equatorial, more rarely with 4-7 evenly distributed pores. Other important characters are the actinomorphic or subactinomorphic corolla with its in the bud contorted lobes. The arrangement of the flowers is very variable : they may be axillary or combined in axillary or terminal, cymose or racemose inflorescences. This subtribe comprises a comparatively large number of genera and is pantropical. From the genera which Lindau included in his *Ruellieae Whitfieldia* and *Stylarthropus.* were removed by me to a new tribe, whereas *Physacanthus* was recognized by Clarke as identical with *Haselhoffia* Lindau ; it belongs therefore to the *Haselhoffieae.*

The *Barleriinae* have globose or prolate, sometimes trigonous, reticulate pollen grains provided with 3 equatorial pores. They are the only subtribe in which the stamens are free. Another important feature is the distinctly zygomorphic corolla of which the two upper lobes may be entirely fused, and the quincuncial or, if the upper lobes are united, decussate aestivation of the lobes. Like the *Ruelliinae* they are pantropical, although in the Old World much better represented than in America. The genus *Lepidagathis* and its nearest allies, which by Lindau were included in this group, have been removed by me to a tribe of their own (v. infra).

The *Strobilanthidinae* differ from the other subtribes in the structure of the androecium, the stamens being united in a short tube which is open on the anticous side, by the presence of two fascicles or rows of hairs on the posticous side of the corolla by which the style is retained against the latter, and in the laterally compressed anticous stigma lobe. The pollen grains are globose or prolate, porate or colporate, usually provided with three equatorial pores, more rarely with 2 or 5, mostly with equidistant and equal bands, more rarely reticulate or spinulose ; in the banded pollen grains the pores are always found between the bands and never, as in the *Petalidiinae* on the latter, and the bands may be punctate, very rarely costate, often septate and sometimes by the suppression of the septa reduced to the elevated margin. The inflorescence is in this subtribe always terminal and racemiform. The number of genera is considerable, but their area of distribution is rather restricted ; it comprises the tropical and subtropical parts of Asia, tropical Australia and Melanesia. The genera with cymose inflorescences which were included by Lindau in his *Strobilantheae* lack the characteristic features of the subtribe and are to be transferred to the *Petalidiinae*.

The *Petalidiinae* are, as a rule, provided with axillary cymes ; occasionally, however, the cymes are combined into a terminal panicle. The corolla is subactinomorphic and never provided with bundles or rows of hairs for retaining the style. The stamens are united in pairs. The anticous stigma lobe is dorsiventrally flattened. The pollen grains are prolate and banded, and three of the bands are in the equatorial plane dilated and contain a pore. Most of the genera are confined to Tropical Africa, but some of them are represented also in Asia, and *Dyschoriste* is pantropical. As stated already, of the genera included by Lindau in this group, *Blechum* has been removed to a subtribe of its own, whereas a considerable part of the genera included by him in his *Strobilantheae*, have to be inserted here.

The *Hygrophilinae* resemble the *Petalidiinae* in the arrangement of the flowers, but the corolla is bilabiate and the stamens are, as in the *Strobilanthidinae*, united in a single group. The pollen grains are globose or subglobose, banded and usually 4-, more rarely 3-colporate ; the bands are equal and equidistant. The style is not retained against the wall of the corolla by rows or bundles of hairs, and the anticous stigma lobe is filiform. The type genus is pantropical, but the other genera are all confined to the Old World. The genera *Eremomastax* and *Mellera*, which were included in this group by Lindau, are apparently to be transferred to the *Petalidiinae*.

As I have advocated already in Dansk Botanisk Arkiv 20 : 75, 1961, the delimitation of the *Lepidagathideae* as given by me in Blumea 10 : 155, 1960, has to be widened somewhat to receive the *Borneacantheae* and the genus *Chroesthes*. In this widened sense this tribe may be defined as follows. The corolla is bilabiate with an emarginate upper lip and a 3-fid lower one, and in the bud the lateral lobes cover the wider and at the base not rarely auriculate central one ; there are four stamens, all with bithecous anthers or, rarely (*Kulemacanthus* v. infra), the inner ones with monothecous anthers, and the pollen grains are minutely reticulate or smooth and 3-colporate, the colpi being short and wide, usually more or less rhomboid ; the ovary cells contain each two ovules, and the stigma is small and bilobate. The distribution is pantropical.

The subtribe *Lepidagathidinae* (tribe *Lepidagathideae* Brem., Blumea 10 : 155, 1960) differs from the two other subtribes by the inequality of the calyx lobes, of which the two anticous ones are partly united. Other important characters are the non-stipitate, not compressed capsule and the densely hairy seedcoat. The distribution of this subtribe which comprises several genera, is pantropical.

The subtribe *Chroesthidinae* contains but a single genus, viz. *Chroesthes* R. Ben., and is still imperfectly known. It differs from the *Lepidagathidinae* in the entirely free anticous calyx lobes, a character in which it resembles the *Borneacanthinae*, the capsule which has been described as compressed, and the seeds which are said to be minutely puberulous, and from the *Borneacanthinae* in the estipitate capsule and the minutely puberulous seeds. The genus *Chroesthes* is confined to Indo-China.

The subtribe *Borneanthinae* (tribe *Borneacantheae* Brem., Blumea 10 : 155, 1960) differ from the two other subtribes in the stipitate capsule and the entirely glabrous seeds. In the entirely free anticous calyx lobes they resemble the *Chroesthidinae*. The type genus is known only from Borneo, but it is not impossible that the imperfectly known genus *Hulemacanthus* S. Moore, which is found in New Guinea, may also belong here (Bremekamp l.c.). The capsule is still unknown. In the structure of the androecium it differs from all *Lepidagathideae* that so far are known, as the inner stamens are monothecous.

The *Andrographideae* and the *Justicieae* differ from the preceding tribes of the *Ruellioideae* in the cochlear aestivation shown by the lobes of the always zygomorphic and usually distinctly bilabiate corolla. That their seeds are never covered by unicellular hairs is also noteworthy, although in the other tribes too glabrous seeds may be found, in the *Ruellieae* and *Lepidagathideae* occasionally and in the *Trichanthereae* even always.

The *Andrographideae* differ from the *Justicieae* in the presence of six or more ovules in each of the ovary cells, in the estipitate capsule and in the structure of the pollen grains, which are 3-colporate with the colpi surrounded by a thickened rim, but the area between the colpi without colpoid streaks are other differentiation. They comprise but a small number of genera and are confined to Tropical Asia.

The *Justicieae* in the delimitation accepted by me comprise the *Asystasieae, Graptophylleae, Pseuderanthemeae, Odontonemeae, Isoglosseáe* and *Justicieae* of Lindau. They differ from the *Andrographideae* in the presence of only two ovules in the ovary cells, the more or less distinctly stipitate capsules and in the structure of the pollen grains which are never of the type described above. If the globose or radially symmetric prolate grains which outside the pores are covered with evenly distributed spinules, a pattern which returns in different circles of affinity and by which, as I have already pointed out, the structure which is characteristic for these groups, is entirely suppressed, are left out of consideration, the pollen grains found in this tribe appear to belong in the main to three different types. The first is a globose or prolate 3-colporate type in which the colpi are accompanied on each side by a colpoid streak ; it is found in the typical representatives of Lindau's *Graptophylleae, Pseuderanthemeae* and *Odontonemeae.* The second type is lenticular with a pore in the centre of each of the flattened sides, and a marginal zone differing in structure from the rest of the wall ; it is found in the typical representatives of what Lindau calls the *Isoglosseae Isoglossinae*, i.e. in my *Rhytiglossinae.* The third type is prolate and dorsiventrally flattened with a pore in the middle of a "trema area" studded with circular "insulae" and extending in the central part of the flattened side from one pole to the other ; it is found in the typical representatives of Lindau's *Justicieae,* my *Justiciinae.* Besides these more common types some other ones are found, e.g. that of *Brachystephanus,* (see Bhoj Raj, Grana Palynologica 3 : 59 and Pl. 8, figs. 1-4), that of *Poikilacanthus* (Bhoj Raj, op. cit. 59 and Pl. 22, figs. 1-4), and that of *Chlamydocardia* (Bhoj Raj, op. cit. 51 and Pl. 10, figs. 1-3), but as the other characters of these genera have as yet not been studied in sufficient detail, their position remains uncertain. Less strongly deviating are the pollen grains found in *Drejerella,* a genus which on account of its near affinity to *Beloperone* is to be included in the *Justiciinae.* These pollen grains are provided with 3 instead of 2 pores, and they are trigonous instead of bilateral. The pores, however, are just as in the *Justiciinae* of the ordinary type situated in a trema area studded with insulae. The last-named character is therefore apparently of greater taxonomic value than the number of pores. In *Gendarussa* too the pollen grains are provided with 3 pores each situated in a trema area, but here the latter is not studded with insulae. This genus too is to be included in the *Justiciinae.* A slight deviation from the type found in Lindau's *Graptophylleae, Pseuderanthemeae* and *Odontonemeae* is found in the genus *Asystasia,* though not in the other genera which were included by Lindau in his *Asystasieae.* The colpi are here longer than they are in Lindau's *Graptophylleae, Pseuderanthemeae* and *Odontonemeae,* and almost fused at the poles, and the bands by which the colpi are surrounded, are dilated round the pores ; the grains, moreover, are distinctly trigonous, in one of the species even slightly tricostate.

For the time being the best solution seems to be to unite the typical representatives of Lindau's *Asystasieae, Graptophylleae, Pseuderanthemeae* and *Odontonemeae* in a single subtribe for which I propose the name *Odontoneminae,* to retain his *Isoglosseae Isoglossinae* as a subtribe *Rhytiglossinae,* the name *Isoglossa* being a younger synonym of *Rhytiglossa,* and his *Justicieae* as a subtribe *Justiciinae.* Some of the genera with aberrant pollen type, like the above mentioned *Brachystephanus, Poikilacanthus* and *Chlamydocardia,* will probably have to be referred to subtribes of their own, but so long as these genera have not been studied in more detail, it seems better to regard them as "genera incertae sedis". The three subtribes may be characterized as follows.

The *Odontoneminae* have a corolla without rugula, i.e. without the two ridges at the posticous side by which in the *Justiciinae* the style is kept in its place, either four stamens or two stamens and two staminodes, bithecous or rarely, monothecous anthers, but in the first case always with the thecae inserted at the same height, and pollen grains provided with colpoid streaks. They are pantropical.

The *Rhytiglossinae* have, like the *Odontoneminae,* a corolla without rugula, while they differ from them in the structure of the androecium, which consists of two stamens not accompanied by staminodes, and in the bithecous anthers of which the thecae are inserted at unequal height. In these characters they resemble the *Justiciinae* : In the lenticular, 2-porous pollen grains they differ from both. Another important character is the presence of tracheidal thickenings in the cells of the testa, but the latter are found also in some of the *Justiciinae*. This subtribe comprises but a small number of genera, and is confined to the Old World.

The *Justiciinae* have a corolla provided with a rugula, and in this respect they differ from the two other subtribes. In the structure of the androecium they resemble the *Rhytiglossinae,* but they differ from them in the structure of the pollen grains, which are always prolate and either bilateral or, more rarely, trigonous, but always provided with pores situated in a trema area. This subtribe is, like the *Odontoneminae,* pantropical and comprises a large number of genera.

Whether it would be possible to distinguish within these subtribes some smaller groups, is difficult to say. Nees already distinguished a group *Dicliptereae,* although we must add that this was in the delimitation accepted by him, a rather heterogeneous mixture. Lindau's *Odontonemeae, Diclipterinae* were a more natural group, although the genus *Rungia,* which he like Nees included here, probably because it resembles *Dicliptera* in the structure and mode of dehiscence of the capsule, does certainly not belong to the subtribe *Odontoneminae,* as it is on account of the presence of a rugula, the structure of the androecium and of the pollen grains to be included in the *Justiciinae.* Moreover, the involucre, the characteristic feature of this group of genera, is absent in *Rungia.* Whether this involucre is everywhere in this group of the same morphological value, is as yet not fully certain. Another rather aberrant genus is *Herpetacanthus,* which Lindau included in his *Isoglossinae,* but which because of the presence of colpoid streaks in the pollen grains, is to be transferred to the *Odontoneminae.* However, on account of the very unusual structure of the inflorescence it occupies a rather isolated position in this subtribe. The inflorescence is spiciform with two bracts at each node, but these bracts are not decussate, but inserted side by side. As at the lowermost node but a single bract is found, it looks as if the second bract has been shifted to the second node, and that at each of the following nodes too one of the bracts has made its way to the next. Howsoever this may be, the structure of the spike is a most unusual one. Another important feature of this genus, though not confined to it, is the presence of four stamens of which the inner ones have monothecous anthers.

I will not say that the classification of the *Justicieae* given above, is perfect. On the contrary, I am convinced that it is no more than a tentative effort. However, before a better one can be evolved, a large number of the genera will have to be reinvestigated. Apart from the characters of the pollen grains attention will have to be paid to the structure and position of the inflorescence, to the presence or absence of a rugula, to the structure of the testa, and perhaps to the shape and distribution of the cystoliths. The chromosome number too might give valuable indications, but as most of the species are available only in the form of herbarium specimens, it will be difficult to obtain the necessary data.

SUMMARY

In this paper the author summarizes and extends his speculations on the delimitation and subdivision of the Acanthaceae. After defending once more the transfer of Lindau's *Nelsonioideae* to the *Scrophulariaceae* and after reaffirming his view that Lindau's *Thunbergioideae* and *Mendoncioideae* are to be raised to family rank, he divides the *Acanthaceae* s.s. into two subfamilies, the *Acanthoideae* and the *Ruellioideae.* In the *Acanthoideae* five tribes are distinguished, the *Haselhoffieae, Rhombochlamydeae, Stenandriopsideae, Aphelandreae* and *Acantheae,* and in the *Ruellioideae* seven, the *Trichanthereae, Whitfieldieae, Louteridieae, Ruellieae, Lepidagathideae, Andrographideae* and *Justicieae.* In the *Ruellieae,* six subtribes are recognized, the *Blechinae, Ruelliinae, Barleriinae, Strobilanthidinae, Petalidiinae* and *Hygrophylinae,* in the *Lepidagathideae* three, the *Lepidathidinae, Chroesthidinae* and *Borneacanthinae,* and in the *Justicieae* three, the *Odontoneminae, Rhytiglossinae* and *Justiciinae.* However, our knowledge of the tribe *Justicieae* is still very incomplete, and the exact position of several of its genera remains uncertain.